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THE MEGASPOROPHYLL OF SAXEGOTHAEA AND MICROCACHRYS

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(WITH PLATES XXII–XXV)

In the Coniferae great importance attaches to "inverse orientation" as a criterion for determining the character of the fertile scale in the megasporangiate cone. The followers of BRAUN see in the inversion of the ovuliferous scale bundles an indication of the "brachyblast" character of this structure. SACHS and EICHLER, the exponents of the "ligular" theory, look upon the inversion as a feature which characterizes the vascularization of a ligule or of an appendage of the simple sporophyll. CELAKOVSKY partly combines the two views and seems to homologize many of the diversified megasporangiate features of the gymnosperms. In the present study some neglected phases of the inversion of the sporangial supply bundles of both the staminate and ovulate cones are given prominence, and data are advanced to show the homology of the micro- and megasporophyll in Saxegothaea and Microcachrys.

The gross features of a fruiting branch of Saxegothaea are indicated in *fig. 1*. The megasporangiate cones are borne terminally on the branches (*figs. 1, 2*), the microsporangiate ordinarily in the axils of foliage leaves, but occasionally in a terminal position (*fig. 3*). The megasporangiate cone, at the stage indicated in *fig. 2*, has a short pedicel beset with the bracts which earlier inclosed it. Later the pedicel elongates and a lax arrangement of the bracts is evident (*fig. 4*). Still later the pedicel becomes much more elongated and relatively very slender. The bracts, sporophylls, and foliage leaves are spirally arranged, and gradations in form are evident, the bracts gradating apically into sporophylls and basally into vegetative leaves (*fig. 4*). The microsporangiate cones may be either sessile or pedicellate. In either case there is a series of spirally arranged bracts closely investing the base of the cone, the lower part of the pedicel, when present, being naked (*figs. 2, 3*). In an otherwise abnormal cone I found the arrangement of bracts similar to that on the megasporangiate pedicel.

The gross features of Microcachrys are indicated in a figure of a previous article.[1] The cones are always terminal in this form and their sporophylls verticillate, in series of fours, the series alternating with one another and presenting from the exterior an appearance of a spiral arrangement (*figs. 5, 6*). The small concrescent foliage leaves are opposite, in alternating pairs.

The form and structure of the microsporophyll of Saxegothaea are indicated in *figs. 7–9*. Two are shown cut longitudinally (*fig. 7*), and between these is one cut through the sporangium, showing the stomium and the wall with its columnar, comparatively thick-walled, epidermal cells. The inner layers of the wall have collapsed, but there are indications of three or four of these.[2] In the axial sections the vascular bundle with its accompanying resin duct is seen, and the connection of these with those of the axis of the cone. The resin canal is expanded distally. This is apparent in the tangential section of the cone as well (*fig. 9*), where the central sporangia often show little trace of a canal, while in the lateral ones it is large. In *fig. 8* resin canals and vascular bundles are seen in transverse sections of the cone, at various distances from the axial supply. In some of the sporangia, to the right of the figure, the position of the stomia is indicated. The microspores contain three cells at the stage from which these figures were made. Megasporangiate cones of the same date have not differentiated the megaspore (*figs. 10, 11*), with the exception of some abnormal ovules, to be described later. A single bundle accompanied by a resin canal passes into each sporophyll, and this gives off the ovular supply just as the point of insertion of the integument is reached

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[1] THOMSON, R. B., On the pollen of Microcachrys. BOT. GAZETTE **47**:26–29. *pls. 1, 2.* 1909. See *pl. 1.*

[2] Cf. NORÉN, C. O., Zur Kenntnis der Entwicklung von *Saxegothaea conspicua* Lindl. Svensk. Bot. Tidskr. **2**:101–122. *pls. 7–9.* 1908.

(*fig. 11*). *Fig. 12* is a transverse section of the sporophyll a little nearer the cone axis than the point indicated. It shows a single vascular bundle, and below it the accompanying resin duct. The wood (lighter in the figure) is roughly triangular in outline. Near its center are two very darkly nucleate cells. These mark the separation of the wood of the ovular supply from that of the main bundle. The bast above this is but slightly differentiated, and nearer to the axis of the cone dies out completely, as does the wood itself in its further course through the cortex. Under the base of the ovule the bast is quite apparent on the upper side of the supply bundle (*fig. 11*), which shows a tendency to bifurcate, the branches passing laterallv into the base of the integument. Beyond the separation of the ovular supply, the main bundle gradually acquires a new set of centripetal wood elements, the more central ones of which are elongated, the lateral quite typical transfusion tissue.

In material of Saxegothaea some six months older than the former, the vascular system of the megasporophyll is further developed. It has been recently described by Miss STILES,[3] with whose account my own observations are practically in accord. The upper vascular system may be composed, in the region of the ovule, of as many as four strands. These, however, in all the material I examined, unite into two before passing upward into the base of the ovule. Miss STILES speaks of there being about three bundles in this region. The pair terminates at the level of the base of the nucellus in a considerable expansion of transfusion-like tissue. The main bundle of the sporophyll is replaced by a series somewhat similar in the same region in which the proliferation of the ovular set occurs. Above the ovule a single bundle is found, with centripetal, and on its flanks a considerable, development of xylem elements. The vascular supply for the scale cones from the axis is a single bundle with normally oriented wood and bast. In the cortex gradually new xylem elements are formed opposite the protoxylem. Farther out wood and bast coming off the sides of the main bundle supplement the original central elements, which up to this point appear not to have any bast of their own. In the further course the proliferation of the upper and lower series occurs, as described above. All of the upper series of bundles pass into the base of the ovule, the only xylem elements found beyond the ovule in this region being a new development associated with the main bundle. A single resin duct accompanies the latter throughout its course. This does not branch and is the only representative of the tissue in the scale, no canals being formed in connection with the upper series of bundles.[4]

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[3] STILES, W., The anatomy of *Saxegothaea conspicua* Lindl. New Phytol. **7**:209–222. 1908.

The vascular system of the axis of the megasporangiate cone consists of a ring of collateral bundles very similar in general to that of the microsporangiate cone (*fig. 8*). The wood of these is usually of the ordinary endarch type, but near the base of the cone there are often a few centripetal elements associated with the bundles at the sides of the gap left by the exit of the megasporophyll trace. In one instance these were almost in continuity with the wood elements of the ovular supply in the sporophyll. The latter, especially in its young condition, appears very much of the nature of centripetal xylem (*fig. 12*),[5] and the occurrence of the isolated elements in the axis affords confirmation of this idea. They are found also in the upper part of the pedicel, but in my material they are rare here.

The scales at the base of the micro- and megasporangiate cones and the foliage leaves both receive a single vascular bundle and a single resin duct from the axis, the supply coming off in a similar way to that of the sporophylls. There is always a gap in the cylindrical stele opposite the "trace" to each of these members (*fig. 8*, for microsporophylls, lower right hand side, etc.).

In several of the megasporangiate cones of Saxegothaea a few of the lower sporophylls bear ovules on their under surface (*fig. 10*). These have an integument, but not the epimatium or rudimentary second integument of the normal ovule. They stand out too from the sporophyll more freely, and are further developed than the upper ones in the same cone. A slight vascular supply goes off to some of these, the bast and wood showing a tendency to orient itself inversely to that of the main bundle of the scale. This supply passes around the resin duct.

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[4] Cf. STILES, *l. c.* 216.

[5] Miss STILES has come to a similar conclusion from studying the more mature condition.

In Microcachrys a single vascular bundle supplies leaf and sporophyll. There are no resin canals in the stem nor in the axis of either cone. It is not until well out into the sporophyll that a canal is found beneath the vascular bundle (megasporophyll, *fig. 13*). The canal of the vegetative leaf, however, is continued downward into its swollen base, and the leaves being concrescent, there is the appearance of resin ducts in the stem. The vascular bundle in both leaf and sporophyll runs closer to the upper than the lower surface. A comparison of longitudinal sections of the megasporophyll and vegetative leaf shows a great resemblance between the distal part of the former and the whole of the latter. There is a distinct palisade on the lower surface of each, a sclerotic hypoderma, and an epidermis with a very thick cuticle and no stomata, the latter being restricted to the upper surface, and in the case of the sporophyll, so far as I have observed, to the region beyond the ovule. There is no hypoderma on the upper surface, and the same kind of degenerate-looking palisade tissue occurs in both sporophyll and leaf. Proximally the sporophyll is contracted into a slender stalk, while the leaf is concrescent with the stem. The vascular supply of the ovule originates in much the same way as in Saxegothaea with at first no apparent bast[6] (*fig. 14;* above the resin canal come bast and wood of the main bundle and above the center of the latter the few wood elements of the ovular supply). On separation the ovular supply bundle passes obliquely upward, as in Saxegothaea (cf. *figs. 11* and *13*), with bast clearly evident on its upper side. In Microcachrys, the single supply bundle bifurcates near the base of the ovule, the divisions passing well into the basal part of the integument.

In most of my material the megaspore of the ovules has only a few nuclei in a parietal stratum of protoplasm (*fig. 13*). In one case, however, a prothallial tissue (*fig. 15*) is present with the archegonial initials discernible. These are located at considerable distances from one another. Around the prothallium the megaspore-coat is of the usual double type.[7] It is slightly thicker than in *Pinus resinosa* at a similar stage. Like the pine coat at this young stage, it is of uniform distribution about the prothallium. It would be interesting to know the condition in the mature seed, especially in view of the fact that in certain species of Dacrydium the megaspore coat is very thick at a later stage.

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[6] Cf. WORSDELL, Observations on the vascular system of the female flowers of the Coniferae. Annals of Botany **13**:538. 1899.

[7] THOMSON, R. B., The megaspore-membrane of the gymnosperms. Univ. of Toronto Studies, Biol. Ser. **4**:1–64. *pls. 1–5.* 1905.

The integuments of the ovule are seen in their usual form in *fig. 13*. Sometimes the inner one is quite open above the ovule (*fig. 15*), even at an advanced stage. In the case figured it is developed laterally into two large masses, appearing as additional ovules in gross material. In other cases it may be uniformly quite thick (*fig. 16*). The two outer cell layers of the integument are tangentially elongated in the older condition, while the third consists of columnar cells radially placed, many of which in the basal region become lignified and have numerous large pits. They are in connection with the supply bundles of the ovule through transfusion-like extensions of the latter.

Fig. 17 is of a longitudinal section of the bract and scale from the megasporangiate cone of *Tsuga canadensis*. The section passes to one side of the axis in the region of the ovule. To the lower right-hand side of the figure the bract is seen fused proximally with the tissues at the base of the scale. The latter shows one large vascular bundle, cut nearly transversely. This has the wood below and the bast above, an arrangement the inverse of that in the bract. From this bundle is given off the ovular supply, which passes obliquely upward into the base of the sporangium. The character of the supply bundle was studied in series of transverse sections. It comes off from one of the lateral bundles of the scale (*fig. 15*; second bundle from the right and left of the figure). Its wood and bast lie at first in a plane at right angles to that of the scale bundles (*fig. 19*; the wood is the small-celled tissue in the center of the figure and the bast is to the left). Shortly the bundle turns completely round, so that its wood lies above and its bast below, the inverse arrangement to that of the scale bundles, which, in turn, is inverse to that of the bract. Near the ovule the bundle becomes concentric and finally bifurcates, the branches entering the base of the integument.

In the microsporophyll of the cycads THIBOUT[8] has called attention to the inverse orientation of the sporangial supply. I have

[8] THIBOUT, E., Recherches sur l'appareil mâle des gymnospermes. pp. 265. *pls. 16*. Lille. 1896.

figured that of *Ceratozamia mexicana* (*fig. 21*). In *fig. 21* the upper bundle is one of the normally oriented main bundles—bast below and wood above, not shown in the section—while cutting obliquely across the field is a sporangial supply bundle with bast above and wood below. A short ventral extension to the sporangia turns at right angles at first and then becomes almost inverse. *Figs. 22* and *23* are transverse sections of a sporophyll. In the upper part of the figures are the main bundles, with wood above and bast below. Farther down and toward the ends of the normal series are some inversely oriented bundles. One, to the left, magnified in *fig. 23*, has just divided into a similarly oriented bundle, and from this there is a strand to the sporangium. The latter has a more or less concentric character. In some cases I have found a second inversion on the way to the sporangia.

The inversion of microsporangial supply bundles is of wide occurrence in the cycads, but is not confined to the group, being also found in certain conifers. This feature has not been considered by the exponents of the theories advanced to explain the inversion in the fertile scale of the latter. That it is of first importance seems self-evident. Again, the double inversion in the fertile scale has not been explained, and a glance at the figures shows how important the second inversion is, both of itself and in comparison with the single inversion in either Saxegothaea or Microcachrys (cf. *figs. 11*, *13*, and *17*). This and the occurrence of ovules on the lower surface of the scale in Saxegothaea, and their vascularization from the main supply, would seem to be good reason to consider that inverse orientation cannot in all cases be relied upon as evidence of the brachyblast character of the fertile scale. In the last case, we should have the anomaly of the leaf in the axil of the shoot.

Again, in Dacrydium two bundles with orientation inverse to that of the scale supply the ovule. These attach directly to the axis, the three passing close together near the upper surface of the scale. There is, then, in Dacrydium, a form admittedly of a higher type than either Saxegothaea or Microcachrys because of the reduction of the cone, etc., a greater amount of inversion than in the more primitive forms—a puzzling feature certainly in view of the brachyblast theory, but possibly finding its explanation in the greater importance of the ovule in this specialized fructification and in the greater advantage which a direct connection with the axial supply affords. This has its beginning in Saxegothaea and Microcachrys, where the two bundles of the ovular supply have asserted their individuality only part way to the axis, the ovular supply in these forms having possibly originated, as has been suggested, as a revival of the centripetal development of the main bundle.

In view of the facts presented, the writer is led to look upon the fertile scale as a simple structure, the homologue of the microsporophyll in both Saxegothaea and Microcachrys, and, *ipso facto*, in the whole of the Taxaceae, if these form a natural alliance, as is commonly held. With this group is to be associated the Araucarieae, whose microsporophylls show an inversion of the sporangial supply bundles of like character to that of the megasporophyll,[9] and which, on other grounds, have been considered[10] as having a simple megasporophyll. This group also has recently been shown to have many features in common with the lower podocarps. Perhaps the most important of these are the method of pollination and the absence of wings on the grains themselves in Saxegothaea and the Araucarieae, the extensive microgametophyte of the two groups, the single inverted ovule, the wide micropyle and projecting nucellus, the nucellus free from the integument to its base—features which bring these forms into intimate association.

The simple-scale groups, the Taxaceae and Araucarieae, have then their micro- and megasporangia on opposite sides of the sporophyll; and since the homosporous forms, from which the conifers were derived, the pteropsid series, as is shown on morphological and anatomical grounds, have the sporangia usually on the lower surface, the ovule has probably been transferred to the upper surface in the course of phylogeny. The ovules on the lower surface of some scales of Saxegothaea and their lateral position in Cycas are significant in this connection, and, as well, the lateral development of the sporangium in Schizaeaceae.

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[9] THOMSON, R. B., The origin of the gymnosperms at the Linnean Society. New Phytol. **5**:145. 1906.

[10] SEWARD, A. C., AND FORD, S. O., The Araucarieae, recent and extinct. Phil. Trans. Roy. Soc. London B. **198**:305–411. *pls. 23, 24.* 1906.

COULTER and CHAMBERLAIN, after reviewing the different theories of the fertile scale in their textbook on the gymnosperms, make the following statement (p. 77): "Upon sifting the testimony certain things seem to be fairly clear, and one is that the scale and its ovules in Abieteae represent a highly modified axillary shoot, corresponding to the characteristic spur shoot of the group." From anatomical and teratological evidence this conclusion seems inevitable, and since the Abieteae, Taxodieae, and Cupresseae present such a series of natural affinities the statement must apply to all. If, then, the fertile scale in this group is of the brachyblast type, representing the adaxially fused first and only two leaves of an abortive axis, the first inversion is explained, and the ovules in this group are borne on the morphologically under surface. The second inversion is analagous to the single one in Saxegothaea and of the nature of a sporangial supply. There are, then, two great groups of the conifers from the standpoint of this study, the simple- and the complex-scale series. Both forms have the ovules on the physiologically upper surface, a position rendered almost imperative by the necessities of the seed habit. This position, however, has been attained in two very different, but possibly equally difficult, ways in the aplo- and diplosporophyllous forms of the Coniferae.

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EXPLANATION OF PLATES XXII–XXV

PLATE XXII

FIG. 1.—Fruiting twig of *Saxegothaea conspicua*. Slightly enlarged.

FIGS. 2, 3.—Micro- and megasporangiate cones. ×4.

PLATE XXIII

FIG. 4.—Megasporangiate cone with the axis more elongated than in *fig. 2*.

FIG. 5.—*Microcachrys tetragona;* micro- and megasporangiate cones, the former in mature condition. ×4.

FIG. 6.—Older megasporangiate cone.

FIGS. 7–9.—Respectively radial, transverse, and tangential sections of the microsporangiate cone of Saxegothaea.

FIGS. 10, 11.—Megasporophylls of Saxegothaea, with ovules attached; *fig. 11* showing ovular supply coming off the main vascular bundle.

PLATE XXIV

FIG. 12.—Transverse section of the megasporophyll of Saxegothaea, young condition, just proximal to the insertion of the ovule.

FIG. 13.—Longitudinal section of the distal part of the megasporophyll of Microcachrys.

FIG. 14.—Transverse section of same, showing ovular and main supply bundles in transverse section.

FIG. 15.—Megasporangium of Microcachrys in transverse section.

FIG. 16.—Sporophyll and megasporangium with abnormally thick integument, in transverse section.

FIG. 17.—*Tsuga canadensis;* bract, scale, and ovule in longitudinal section.

PLATE XXV

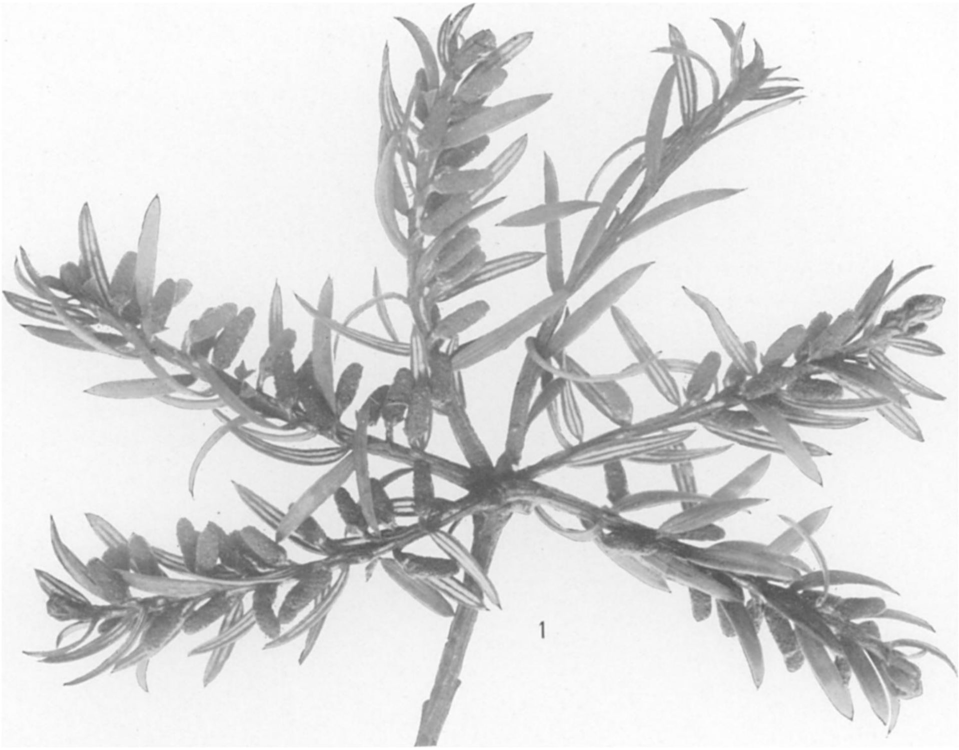
FIG. 18.—*Tsuga canadensis;* transverse section of bract, scale, and ovules at the point of origin of the ovular bundles.

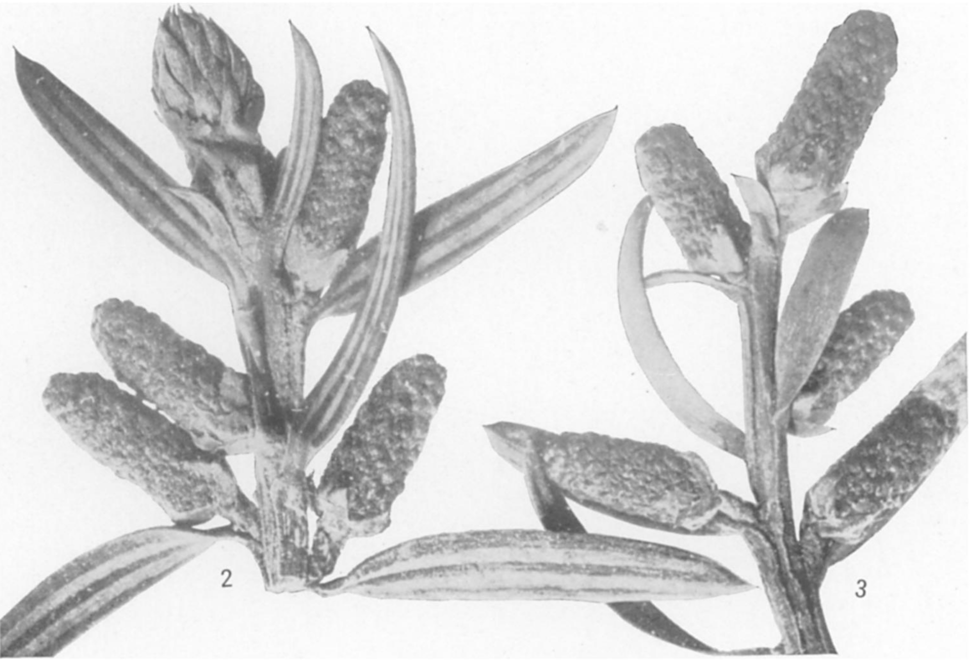
FIG. 19.—The same; a magnification of the ovular supply of the right ovule in *fig. 18.*

FIG. 20.—The same; supply bundle farther up.

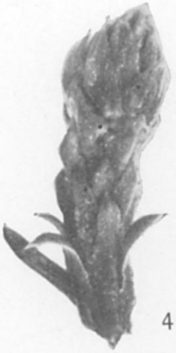
FIGS. 21, 22.—Respectively, longitudinal and transverse sections of microsporophyll of *Ceratozamia mexicana.*

FIG. 23.—A magnification of a part of *fig. 22.*





THOMSON on MEGASPOROPHYLL



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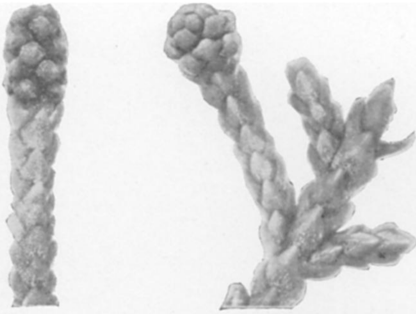

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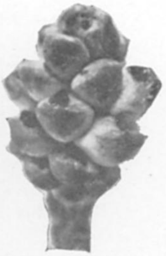

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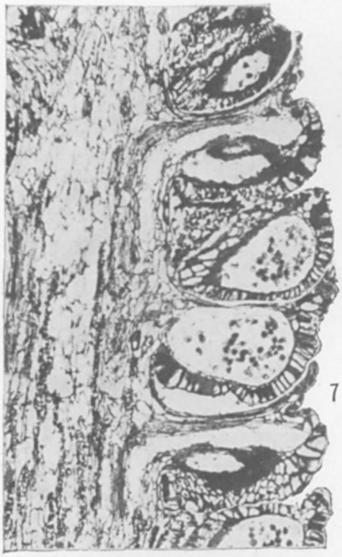

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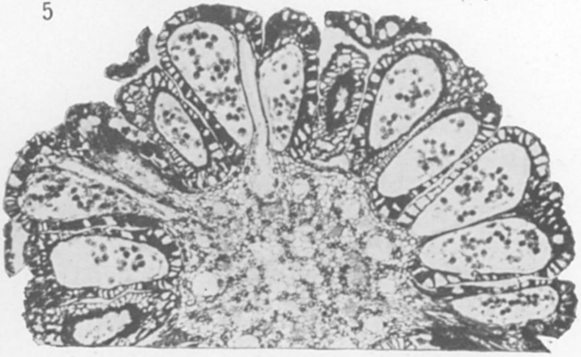

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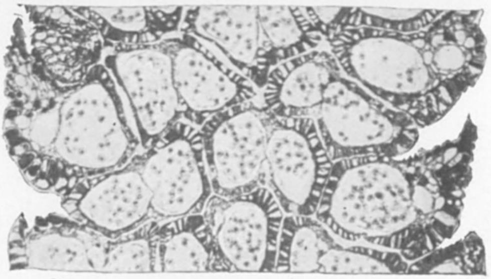

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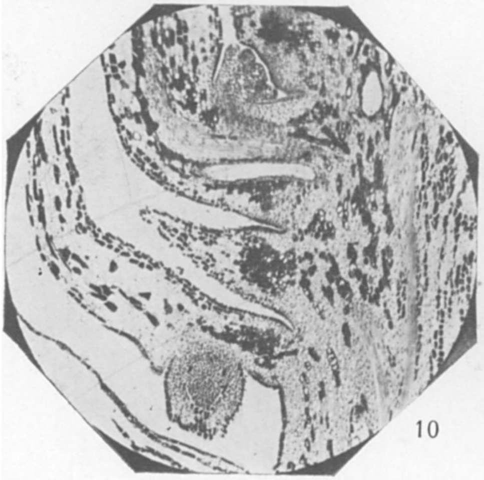

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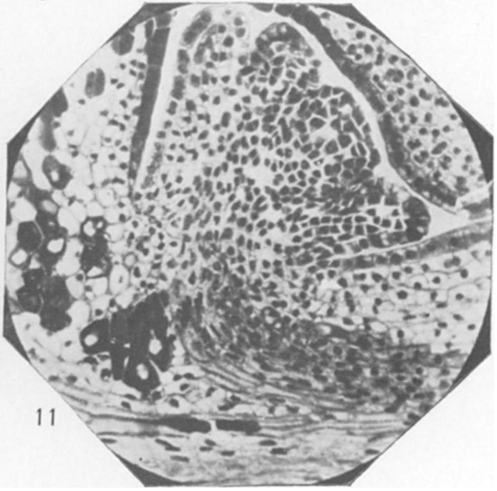

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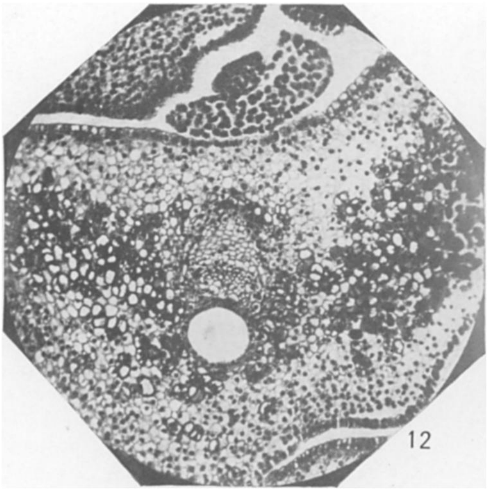
THOMSON on MEGASPOROPHYLL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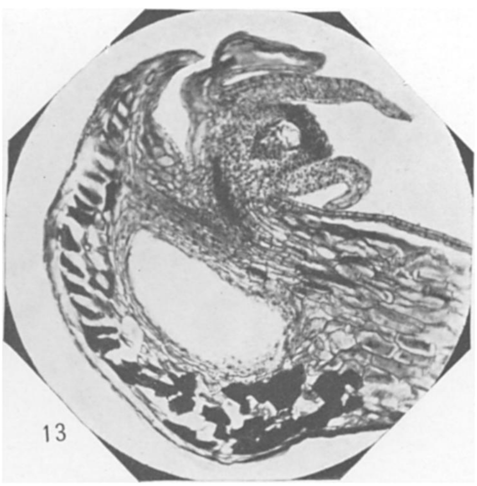
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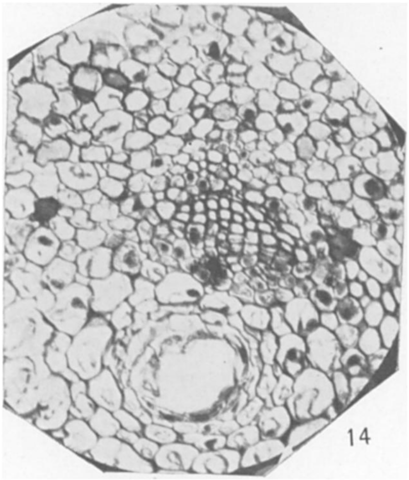
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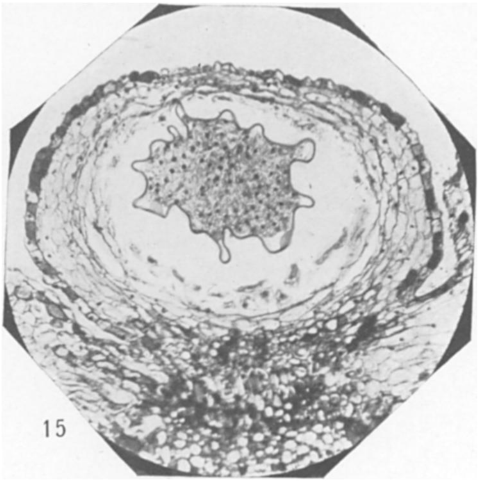
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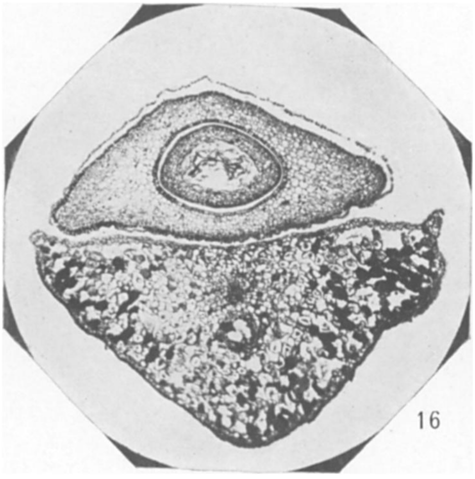
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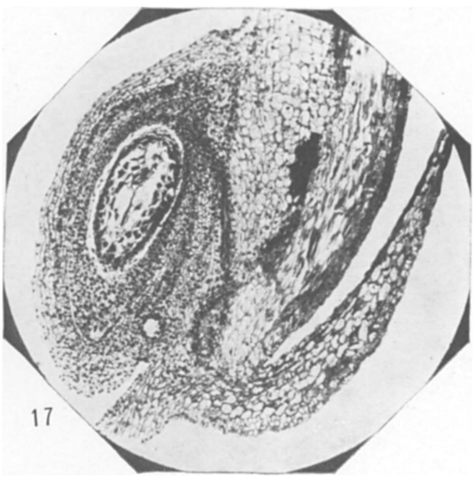
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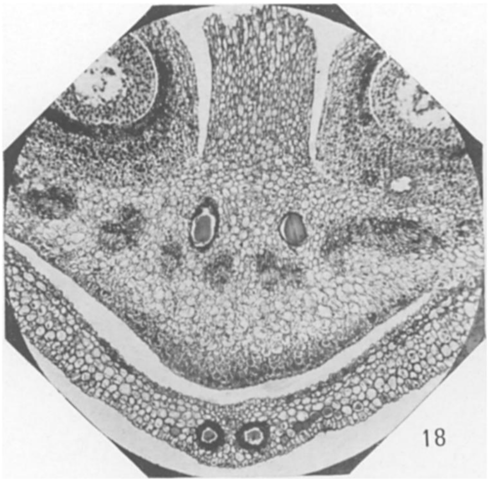
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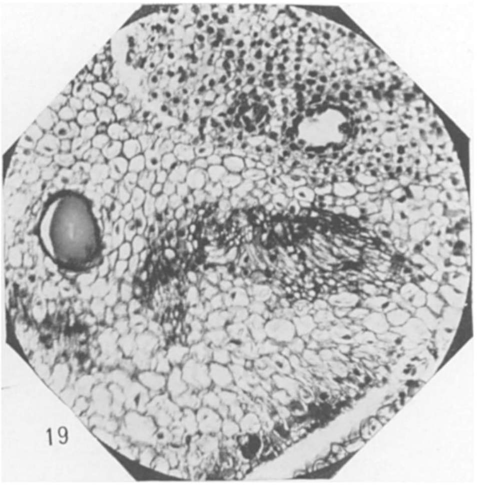
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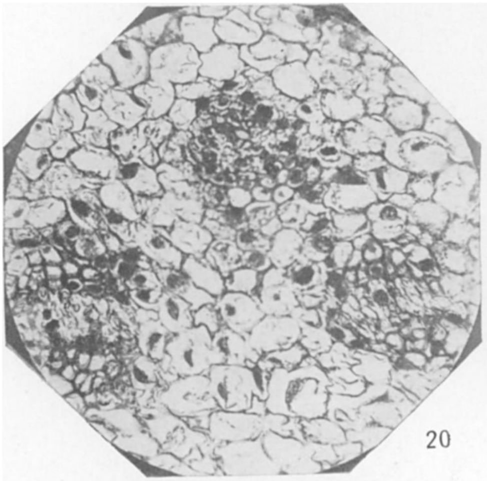
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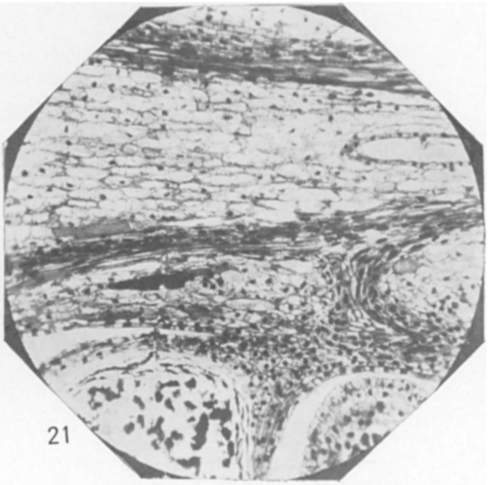
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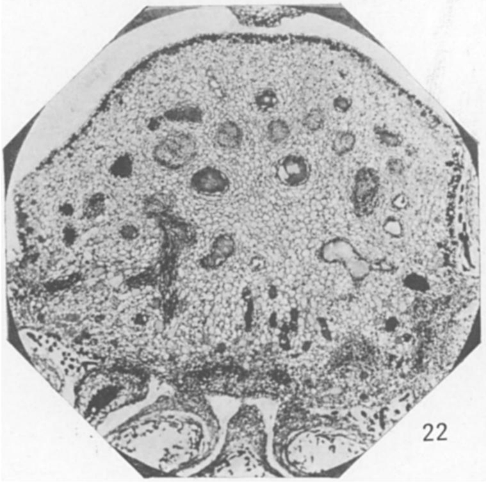
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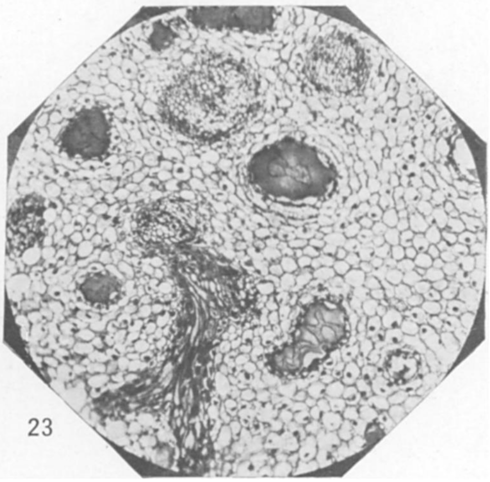
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THOMSON on MEGASPOROPHYLL